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Mammalian Hybrids and Generic Limits

RICHARD G. VAN GELDER[1]

ABSTRACT

A taxonomic level, the genus, is analyzed from the perspective of reproduction isolation. It is concluded that if species are, by definition, reproductively isolated, then species in one genus should not be capable of breeding with species in other genera. A survey of reported mammalian intergeneric hybrids and the application of reproductive criteria to the definition of the category of genus led to the recommendation of a number of taxonomic changes in the content of genera. These include the following genera, with synonyms in parentheses: *Macropus* (*Thylogale*, *Osphranter*, *Megaleia*, *Wallabia*); *Cercopithecus* (*Papio*, *Macaca*, *Cercocebus*, *Mandrillus*, *Cynopithecus*, *Theropithecus*, *Erythrocebus*, *Allenopithecus*, *Comopithecus*); *Grampus* (*Steno*, *Tursiops*); *Canis* (*Alopex*, *Urocyon*, *Fennecus*, *Vulpes*, *Cerdocyon*, *Dusicyon*); *Ursus* (*Thalarctos*, *Selenarctos*); *Melursus* (*Helarctos*): *Felis* (*Panthera*); *Arctocephalus* (*Zalophus*); *Tayassu* (*Dicotyles*); *Cervus* (*Dama*, *Axis*, *Elaphurus*); *Bos* (*Bibos*, *Bison*); *Tragelaphus* (*Taurotragus*, *Boocercus*); *Cephalophus* (*Sylvicapra*); *Alcelaphus* (*Damaliscus*, *Beatragus*); *Connochaetes* (*Gorgon*); *Kobus* (*Adenota*, *Onotragus*); *Capra* (*Ovis*, *Ammotragus*).

INTRODUCTION

The genus is a taxonomic level higher than that of a species. It is generally stated that the boundaries of the genus are arbitrary because the criteria for them are wholly subjective. In this way the genus differs from the species, which is presumed to have an objective basis for its construction. This conceptual objectivity is founded on the biological and evolutionary idea that, in order to maintain itself in nature, a species must be reproductively isolated from its close relatives. Prior to the development of this biological or genetic concept of species, taxa of this category were defined mainly on morphological grounds, essentially: a species was composed of individuals that resembled one another more than they resembled any other individuals or groups (or populations). The amount of difference required to distinguish one species from another was not established in this definition, and the determination of species boundaries remained an arbitrary construct of the taxonomist. Essentially the same definition was applied to the genus and to other

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higher categories, each using the next lower category in its definition.

The biological concept of the species (Simpson, 1961, pointed out that the other concepts are also biological) grew from the morphological one. The morphological similarities that characterized species were genetically determined and maintained by gene flow within the species. Reproductive isolation prevented dilution or alteration of the species morph. The biological species concept, based on reproduction, has been attacked because it is inapplicable in some instances (e.g., paleontology) or still permits arbitrariness in the case of forms that are geographically isolated, such as insular ones, and therefore are reproductively isolated. In practice, however, the biological concept is used both by paleontologists and neontologists who deal with geographically or chronologically isolated populations. On the basis of the morphological distinctions between the populations, or actually between samples representing these populations, the taxonomist estimates whether or not, in his opinion, the differences are so great that interbreeding would be impossible if the two came into contact. For the majority of species of mammals, knowledge of reproductive habits is lacking, even within a population. There are some taxonomists who, because of this, would deny the biological concept of the species and return to the purely morphological concept for species (see, for example, Blackwelder, 1967).

It is not the purpose of the present paper to explore the concept of the species, which has a literature of its own. The idea of the species as a distinct unit that is maintained by its own supply of genes, and which is not influenced by the genes of other taxa flowing into it, is one that I accept as fundamental to the understanding of evolution and to the evolution of organisms. I think that most mammalian taxonomists accept the concept of a reproductively isolated species, even if their material does not permit the utilization of reproductive data for determination of species.

The genus, however, is thought to be an arbitrary division, a purely human construction, which may have no real basis in nature. The idea that the genus is constructed for human convenience is clearly evident from such statements as, "In entomology there is sentiment in some quarters for setting an upper limit (perhaps 40) to the number of species allowed in a single genus" (Ross, 1975), or the admonition that the morphological gap between genera should be in inverse ratio to the size of the group (Mayr, Linsley, and Usinger, 1953), size here being taken as the number of species. Despite its limited or nonexistent objectivity, the idea of groups of species arranged in genera is a useful one, so much so that Simpson (1945) said "the genus is, on the whole, the most definite and permanent unit of modern classification, to such an extent that the genus may be considered the basic unit of practical and morphological taxonomy, although the species is the basic unit of theoretical and genetical taxonomy."

A genus is, by definition, composed of one or more species, and it therefore follows that for a genus to exist, its species must exist. In part this portion of the definition derives its basis from nomenclature, in that a species name must include its generic name. This historical artifact, however, has no particular bearing on the concept of the genus composed of species. For a species to form, a high degree of reproductive isolation must develop, either through some kind of isolation that permits a genetic change that results in incompatibility, or through a genetic change in a number of individuals within the population that permits them to interbreed among themselves and not with others. Sibling species, which could be the result of the latter mechanism, exist, but it is argued that some other form of isolation—ecological, behavioral, chronological, or physical (geographic)—must have preceded the genetic differentiation. Morphological differences are scant in sibling species.

An essential part of the species definition is that if the populations involved are different species and sympatric or contiguous, they must maintain their genetic integrity *in nature*. If the populations are separated by geographic or ecologic barriers, their *potential* for successful interbreeding becomes the criterion for determining their status as species. "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr, 1942). Thus, reproductive incompatibility in nature is practical as

an objective test only for sympatric and synchronous species, or allopatric species in a zone of contact. For wholly allopatric populations, however, laboratory testing is possible and acceptable to establish the potentiality of interbreeding. For allochronous populations, testing is generally not possible.

Hybrids between species of free-living mammals are rare. In part this may be due to the difficulty of finding and identifying hybrids, but also probably is a result of actual rarity of occurrence, or reduced viability of the hybrids. More often when two presumptive species are found in contact and there is interbreeding, it is determined that there is fairly continuous gene flow and lack of sterility in the hybrids. The two parental "species" are then considered to be only subspecies, rather than species, and the "hybrid" zone to represent an area of intergradation between two subspecies.

Often, when two closely related species come into contact, there tends to be a reinforcement of the characters that distinguish each. This "character displacement" may be more common than hybridization. When hybridization does occur between two species that are sympatric or contiguous in distribution, and if they are valid species, the hybrids are expected to be sterile, or at least to have greatly reduced fertility. Thus, while there may be a flow of genetic material from both parental species into the hybrid population, there is a general lack of flow from one species to the other, conforming with the species definition.

What happens *in nature* is the fundamental criterion for determining the species when two nominal taxa are in contact and have the physical opportunity to interbreed. In the cases of populations that are geographically, ecologically, or otherwise physically isolated, and for which there are no reproductive data even from non-natural conditions, the taxonomist usually judges the relationship of the two taxa on the basis of the amount and kind of morphological difference evident between the two. If the differences are equal to, or less than, those to be found between contiguous subspecies of the taxon, he will generally consider the isolates to be potentially capable of interbreeding and regard them as subspecies. If, however, the amount of difference is greater than between contiguous populations (subspecies) he may well regard the allopatric forms as separate species. Should the mammalogist, in a case of this sort, have the opportunity to cause members of the two taxa to be brought together and if they did interbreed and produce viable offspring, he would then have the opportunity to determine their potentiality for reproduction in drawing his taxonomic conclusion. In general, should the offspring be sterile or show reduced fertility, probably two species would be recognized. If the offspring were fertile, the two allopatric populations probably would be recognized as only subspecifically distinct. In this example, if course, the potential for reproduction has been determined under artificial, not natural conditions, between populations that are not in contact in nature and therefore do not have the opportunity to interbreed. Were the same artificial experiments to be performed with two species that occur together in nature, and which are not known to interbreed, the production of viable, fertile hybrids under artificial conditions would not deny the specific integrity of both species *in the wild*, and would tend to confirm it. Despite genetic compatibility, the species maintain their gene pools by not interbreeding in nature. Since genetic, morphological, physiological, or physical barriers to potential reproduction would have been ruled out by the artificial hybridization, other mechanisms such as behavior or timing would seem to be the ones that keep these species from diluting each other's genes in natural situations.

Thus, at the species level there may be pairs of species that cannot interbreed as well as pairs that can, but do not, interbreed. The latter are those that have been shown to be genetically compatible under artificial conditions, but which, nevertheless, are reproductively separated in nature. The usual morphological criteria would seem to play no role in these cases. Sibling species, almost indistinguishable morphologically, are reproductively incompatible. Species that are seemingly quite distinct, such as lions (*Leo leo*) and leopards (*Leo pardus*), are capable of producing viable offspring in captivity, although they are not known to, or likely to in the wild, where in many places they are sympatric.

Evolutionary proximity is implied by inter-

specific hybrids. Presumably two populations that become geographically separated could go their own evolutionary ways and yet maintain the potential for interbreeding for a long time, or until such time as their morphological or physiological differences became so great that the physical production of a viable hybrid was impossible. They could also, once separated, diverge so rapidly morphologically or physiologically, that reproductive incompatibility could be attained in a relatively short period. The element of time is often an unspoken thought in consideration of taxa, but is not necessarily relevant in these considerations. Sibling species could conceivably maintain their identity for the same period of time during which allopatric populations could show remarkable divergence that would lead to their recognition as distinct genera with sufficient physiological or morphological deviation to make hybridization impossible. However, the question that is the subject of this paper is the situation when morphological divergence has taken place to the point where the two populations are considered different genera and hybridization can still occur.

Are intergeneric hybrids possible? Certainly in the literature of mammalogy (Gray, 1972) there are a number of cases of intergeneric hybrids. The question here is whether the taxonomic position of the species involved in these instances of hybridization should be reconsidered. If populations that actually or potentially do not interbreed are considered different species, does it not follow that genera, which are composed of species, must neither actually nor potentially interbreed? The duality of philosophy concerning the species and the higher categories has been pointed out (Simpson, 1961): that the species is "real" while the genus is a human artifact. Nevertheless, the genus and all the other higher categories have within them the fundamental evolutionary reality of the species. Thus, the upper limit for the species (reproductive incompatibility) should also be contained in the definition of the genus, and at least represent its lower limit. This would imply that intergeneric hybrids should not be possible by so defining the genus. The arbitrariness of the definition of the genus exists in its width and upper reaches, not at its interface with the species, where its definition is the same as that of a species. Surely we should question our criteria for genera when we have rather similar (morphologically) species that cannot interbreed and highly distinctive (morphologically) entities that we call genera but which are still evolutionarily so proximate that they are potentially and actually capable of interbreeding.

To a large extent our concepts of genera are based on tradition and comfortable familiarity, rather than science. The retention of the genus *Bison*, for example, is largely traditional. I have spoken with many mammalogists about the fact that not only are the two "species" *B. bison* and *B. bonasus* interfertile in both sexes, but members of the "genus" *Bison* can also hybridize and produce viable offspring with various members of the "genus" *Bos*, including the gayal (*B. frontalis*), the yak (*B. grunniens*), and western cattle (*B. taurus*). All agreed that two species of bison probably should not be recognized, but only Haltenorth (1963) followed by Koopman (1967) seem to have adopted this. Virtually all mammalogists agree verbally that "*Bison*" and "*Bos*" are congeneric. Tradition weighs so heavily, however, that I cannot find "*Bos bison*" regularly used anywhere in the recent literature and even I, although I had thought of them as being congeneric long ago, am guilty of using *Bison*, as a *lapsus mentali* (Van Gelder, 1969).

Few mammalogists have dealt with the question of the taxonomic rank of intergeneric hybrids. Simpson (1961) commented "Even without direct knowledge of genetic constitution, successful hybridization is practically conclusive proof of chromosomal equivalence and secondarily of the homologous nature of the structural similaries." He was discussing, however, homologies between species and subspecies, but went on in a footnote: "Supposedly intergeneric hybridization, usually with sterile offspring, is possible among animals, for instance in mammals, the artificial crosses, *Bos* × *Bison*, *Equus* × *Asinus*, and *Ursus* × *Thalarctos*. In my opinion, however, this might better be taken as basis for uniting the nominal genera. I would not now give generic rank to *Bison*, *Asinus*, or *Thalarctos*." In his 1945 classification, Simpson gave generic status to *Bison* and *Thalarctos*, and listed *Asinus* as a probable subgenus of *Equus*.

Buettner-Janusch (1966) utilized the information on hybrids to suggest combining the primate genera *Papio* and *Macaca*, both in a broad sense. "If primates which are presumed to be members of separate genera mate and produce living though sterile offspring, they should be considered members of the same genus."

I have previously raised the question of generic status between the antelopes *Taurotragus* and *Tragelaphus* (Van Gelder, 1977), combining these two as well as *Boocercus* in the genus *Tragelaphus* on the basis of hybridization: "it would seem that if two taxa have achieved the level worthy of generic separation, genetic incompatibility should have occurred, and that intergeneric hybrids should, by definition, be impossible."

MATERIALS AND METHODS

Annie Gray's most useful compilations of sources on mammalian hybrids (1954, 1966, 1972) have served to provide most of my data on intergeneric hybrids. In utilizing this work, I have, wherever possible, gone to original sources cited by Gray to attempt to determine for myself the validity of the claimed hybridization. Unless otherwise mentioned, Gray (1972) is the initial reference for the source of hybridization data and original references. The birth of a living offspring was taken as the criterion for successful hybridization. Where there are doubts concerning the data, suitable comment follows. The genera mentioned here are those used by Gray (1972).

In making recommendations for the allocations of genera, I have selected the earliest valid generic name. In concluding that two or more genera should be merged, I have not required that more than one species of one genus be capable of hybridizing with more than one of the other. An alternative to this, of course, would be to transfer only the species that are known to hybridize, leaving the residue in its original genus. By presenting data on the actual species involved in intergeneric crosses, I have given the reader the opportunity to follow the latter course. Persons doing this, however, should take care to check the nomenclature involved in the transfer, especially to ascertain whether the type species of a genus is being transferred.

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INTERGENERIC HYBRIDS

Gray (1972) listed no records of intergeneric crosses in the orders (as listed by Simpson, 1945) Monotremata, Insectivora, Dermoptera, Chiroptera, Edentata, Pholidota, Tubulidentata, Proboscidea, Hyracoidea, or Sirenia.

MARSUPIALIA

The intergeneric crosses within Marsupialia are known only from the family Macropodidae. Ride (1970) recognized both *Macropus* and *Megaleia* as genera for kangaroos, as did Van Deusen and Jones (1967). Simpson (1945) considered *Megaleia* a synonym of *Macropus*. Crosses in captivity between *Macropus fuliginosus* and *Megaleia rufa* produced hybrids that were sterile (Gray, 1972). Hybrids between *Macropus giganteus* and *Megaleia rufa* have also been produced in captivity.

Gray (1972) reported, under the name *Wallabia elegans* Lambert, a cross with *Macropus giganteus* with hybrids produced in captivity. Ride (1970) listed the former species, *Wallabia elegans*, whose hybridization with *Macropus* was reported by Calaby and Poole (1971) and Richardson, Czuppon, and Sharman (1971), as *Macropus parryi* and did not place this species in the genus *Wallabia*, which he reserved only for *W. bicolor*.

Simpson (1945) recognized *Protemnodon* Owen, 1873, as the generic name for the large wallabies, listing *Wallabia* auct. as a synonym. Van Deusen and Jones (1967) recognized *Wallabia* Trouessart (1911) with a single species, presumably the same as Ride (1970) did, for *W. bicolor*. Since there are known hybrids between *Wallabia bicolor* and *Macropus agilis* of Ride (1970), *Wallabia* would seem to be congeneric

with *Macropus* even in Ride's restricted sense of *Wallabia.*

Gray (1972) also listed crosses of *Megaleia rufa* with *Osphranter robustus* and with *Osphranter antilopinus cervinus.* Both of these representatives of *Osphranter* were included by Ride (1970) in the genus *Macropus*, and Simpson (1945) also considered *Osphranter* a synonym of *Macropus.*

According to Gray (1972) a hybrid was born in the Frankfurt Zoo from a cross between *Thylogale thetis* and *Wallabia rufogrisea frutica.* The latter was considered by Ride (1970) to be in the genus *Macropus*, while he did recognize *T. thetis* as one of three Australian species in the genus *Thylogale.* This cross would question the validity of the genus *Thylogale*, especially in light of the interspecific crosses known between *T. thetis* and one of the other species, *T. stimatica*, in the genus *Thylogale.*

The intergeneric hybrids known for marsupials, then, suggest that the inclusive *Macropus* of Simpson (1945) with *Megaleia* as a synonym was correct. *Wallabia*, which was recognized by Ride (1970) only for *W. bicolor*, would not only be affected by the cross of *Thylogale thetis* with *W. rufogrisea frutica*, which Ride placed in *Macropus*, but the genetic compatibility of *W. bicolor* with *Macropus agilis* also questions the validity of *Wallabia* as a genus. The cross between *Thylogale thetis* and *W. rufogrisea* (=*Macropus*) questions the status of *Thylogale* as a correct generic appelation for the pademelon *T. thetis*, if not for the genus *Thylogale* as a whole.

The generic synonymies for each of the hybrids and the earliest name according to priority are:

Megaleia Gistel, 1848 X *Macropus* Shaw, 1790= *Macropus* Shaw, 1790.

Osphranter, Gould, 1842 X *Macropus* Shaw, 1790=*Macropus* Shaw, 1790.

Megaleia Gistel, 1848 X *Osphranter* Gould, 1842=*Osphranter* Gould, 1842.

Wallabia Trouessart, 1911 X *Thylogale* Gray, 1838=*Thylogale* Gray, 1837.

Wallabia Trouessart, 1911 X *Macropus* Shaw, 1790=*Macropus* Shaw, 1790.

Recommendation. Genus *Macropus* Shaw, 1790, with *Thylogale* Gray, 1837, *Osphranter* Gould, 1842, *Megaleia* Gistel, 1848, and *Wallabia* Trouessart, 1911, as synonyms.

PRIMATES

In the primates there are many intergeneric hybrids recorded, virtually all from the family Cercopithecidae, suggesting that generic splitting has been extensive in this group. Simpson (1945) recognized 10 genera in the subfamily Cercopithecinae: *Macaca*, *Cynopithecus*, *Cercocebus*, *Papio*, *Comopithecus*, *Mandrillus*, *Theropithecus*, *Cercopithecus*, *Allenopithecus*, and *Erythrocebus.* The more recent arrangement of Napier and Napier (1967) was less divided, with *Allenopithecus* included in *Cercopithecus* and *Comopithecus* in *Papio.*

Anderson (1967) recognized only six of the 10 genera listed by Simpson: *Cercocebus*, *Cercopithecus* (including *Allenopithecus* and *Erythrocebus*), *Cynopithecus*, *Macaca*, *Papio* (including *Comopithecus* and *Mandrillus*), and *Theropithecus.*

Allenopithecus nigroviridis has been crossed with *Cercopithecus aethiops* and produced a viable offspring.

Cercocebus atys was successfully crossed with *Macaca fascicularis* as well as with *Macaca nemestrina*, and *Cercocebus torquatus* has been hybridized with *Macaca fascicularis* and with *Macaca nemestrina.* Similarly, *Cercocebus* has been successfully crossed with *Mandrillus*: a living offspring was born, but did not survive, from a cross between *C. torquatus* and *Mandrillus leucophaeus*, and a hybrid between *C. torquatus* and *M. sphinx* survived for four months before dying of diarrhea.

Cercopithecus aethiops has been reported to cross successfully with *Macaca mulatta*, *M. radiata*, and *M. sinica.* A hybrid between *Cercopithecus* (probably *cephus*) and *Erythrocebus patas* was produced in 1960. *Cercopithecus pygerythrus* has been successfully crossed with both *Macaca radiata* and *Macaca sinica*, and *Cercopithecus sabaeus* with *Macaca mulatta.*

Cynopithecus niger has produced living offspring when crossed with *Macaca fascicularis*, *Macaca maurus*, and *Macaca nemestrina.* Fooden (1976) considered the proper names for *C. niger* and *M. maurus* to be *Macaca nigra* and *Macaca maura*, respectively.

In addition to the crosses between the kinds of *Macaca* already mentioned, *Macaca fascicularis* has been crossed successfully both with *Mandrillus leucophaeus* and *Mandrillus sphinx*. *Macaca fascicularis* is supposed also to have been successfully crossed with *Papio cynocephalus*. *Macaca maurus*, when crossed with *Mandrillus leucophaeus*, produced a hybrid that died soon after birth. *Macaca mulatta* was successfully crossed with *Papio hamadryas*, and *Macaca nemestrina* with *P. hamadryas*. No conception seems to have resulted from copulations between *Macaca nemestrina* and *P. anubis*, and a hybrid between *Macaca nemestrina* and *P. ursinus* was born dead. *Macaca nemestrina* is also reported to have produced a hybrid with *Mandrillus leucophaeus*, the offspring dying soon after birth.

Mandrillus leucophaeus has successfully hybridized with *Papio hamadryas* as well as with *Papio papio*, and *M. sphinx* with *Papio anubis* and *P. hamadryas*. *Comopithecus* as a generic name for the hamadryas baboon is not generally used today, and crosses between *P. hamadryas* and *P. anubis* occur in nature in a narrow zone where the two species are in contact. This should lead to consideration of them only as subspecies. *Papio hamadryas* has also produced viable hybrids when crossed with *Papio ursinus* and with *Theropithecus gelada* (Anon., 1975).

It is clear that the 10 genera of cercopithecines that Simpson (1945) recognized are far more closely related than would be indicated by their separation at the generic level. I have not dealt with the numerous interspecific hybrids produced between the various species within the nominal genera, for which Gray (1972) is the best source. To show the connecting lineages, we find the following successful crosses:

Cercopithecus × *Allenopithecus*
× *Erythrocebus*
× *Macaca*
Macaca × *Cynopithecus*
× *Cercocebus*
× *Papio*
× *Comopithecus*
Comopithecus ×
Theropithecus

The generic synonymies for each of these hybrids and the earliest name according to priority are:

Allenopithecus Lang, 1923 × *Cercopithecus* Linneaus, 1758=*Cercopithecus* Linnaeus, 1758.

Cynopithecus Geoffroy St.-Hilaire, 1835 × *Macaca* Lacépède, 1799=*Macaca* Lacépède, 1799.

Erythrocebus Trouessart, 1897 × *Cercopithecus* Linnaeus, 1758=*Cercopithecus* Linnaeus, 1758

Mandrillus Ritgen, 1824 × *Macaca* Lacépède, 1799=*Macaca* Lacépède, 1799.

Theropithecus Geoffroy St.-Hilaire, 1843 × *Papio* Erxleben, 1777=*Papio* Erxleben, 1777.

Mandrillus Ritgen, 1824 × *Cercocebus* Geoffroy St.-Hilaire, 1812=*Cercocebus* Geoffroy St.-Hilaire, 1812.

Cercocebus Geoffroy St.-Hilaire, 1812 × *Macaca* Lacépède, 1799=*Macaca* Lacépède, 1799.

Macaca Lacépède, 1799 × *Papio* Erxleben, 1777=*Papio* Erxleben, 1777.

Macaca Lacépède, 1799 × *Cercopithecus* Linnaeus, 1758=*Cercopithecus* Linnaeus, 1758.

Comopithecus Allen, 1925 × *Theropithecus* Geoffroy St.-Hilaire, 1843=*Theropithecus* Geoffroy St.-Hilaire, 1843.

According to Buettner-Janusch (1966) and Napier and Napier (1967) the first valid use of the name *Papio* was by Müller (1776) for the mandrill. Delson and Napier (1976) cited Müller's (1773) use of *Papio* (as a subgenus) that seemingly included a macaque, a squirrel monkey, and a drill or mandrill. Napier and Napier (1967) and Dandelot (1971) utilized *Papio* Erxleben (1777) for baboons even though some of these authors acknowledge that it is wrong. But because they recognize *Mandrillus* as a genus and the type of *Papio* Müller (1776) is supposedly a mandrill, they believe that stability is enhanced by retaining *Papio* Erxleben for what are popularly called baboons, as opposed to drills and mandrills. Delson and Napier (1976) have appealed to the International Commission on Zoological Nomenclature for a decision regarding these names. They suggest two alternatives: That *Papio* Müller (1773) be retained for the mandrills and that *Chaeropithecus* Gervais (1839) be used for the savannah baboons; or that *Papio* Erxleben (1777) be the name of the savannah baboons and that *Mandrillus* Ritgen (1824) be assigned to the drills and mandrills. The proposal synonymizing "genera" of mandrills with baboons obviates this problem at the generic level, as was pointed out by Buettner-Janusch (1966), with *Papio* Müller

(1776 or 1773) serving as the generic name for both baboons and mandrills.

The congeneracy of *Macaca* and *Papio* not only had been suggested by Buettner-Janusch (1966), but he also suggested that *Cercocebus* might be united with these. Chiarelli (1961) had summarized primate hybrids and noted these intergeneric crosses, but made no recommendation of taxonomic changes. The prime novel suggestion I am presenting here is the union of *Cercopithecus* with the all-inclusive *Papio.* Since Gray (1972) referred to a number of crosses between species of *Cercopithecus* and various species of *Macaca*, and to crosses between species of *Macaca* and various baboons, drills, and mandrills, the union of all of the extant "genera" that were included by Simpson (1945) in the subfamily Cercopithecinae into a single genus seems warranted. The earliest name for this genus would be *Cercopithecus* Linnaeus, 1758. Although Dandelot (1971) retained five genera of cercopithecines for Africa (*Papio*, *Theropithecus*, *Macaca*, *Cercocebus*, and *Cercopithecus*), he commented: "As regards the mangabeys, which are sometimes regarded as African representatives of the Asiatic macaques, it can be assumed that they form the link between *Papio* (*sensu lato*) and *Cercopithecus* (*sensu lato*)."

Recommendation. Genus *Cercopithecus* Linnaeus, 1758, with *Papio* Müller, 1776 or 1773, and *Papio* Erxleben, 1777, *Macaca* Lacépède, 1799, *Cercocebus* Geoffroy St.-Hilaire, 1812, *Mandrillus* Ritgen, 1824, *Cynopithecus* Geoffroy St.-Hilaire, 1835, *Theropithecus* Geoffroy St.-Hilaire, 1843, *Erythrocebus* Trouessart, 1897, *Allenopithecus* Lang, 1923, and *Comopithecus* Allen, 1925, as synonyms.

LAGOMORPHA

Some hybrids between genera of lagomorphs have been reported (Gray, 1972), but all of them were questioned. *Lepus europaeus* × *Oryctolagus cuniculus* hybridization is doubtful because all artificial insemination attempts have resulted in little more than fertilization and development no further than blastocysts. Alleged crosses between other species of *Lepus* and *Oryctolagus cuniculus* are generally doubted by Gray, and all artificial insemination experiments have been unsuccessful in producing offspring.

Attempts to produce hybrids from artificial insemination of *Oryctolagus* with *Sylvilagus* have not been successful.

RODENTIA

Considering the large number of genera in the order Rodentia, it is surprising that there are not more cases of hybridization known. In part this may be because rodents, especially the smaller ones, have not been especially desired by zoos, where most of the hybridization of other species has taken place. Alleged crosses between *Arvicola* and *Mesocricetus*, *Cricetus* and *Mesocricetus*, *Mesocricetus* and *Mus*, *Mesocricetus* and *Rattus*, *Microtus* and *Mus*, and *Mus* and *Jaculus* were all either unsuccessful or are of doubtful validity, according to Gray (1972). The same is true of reports of interordinal crosses between *Rattus norvegicus* and *Oryctolagus cuniculus.*

Gray (1972) cited Gunning's (1901) report of hybridizing *Aethomys chrysophilus* with *Rattus norvegicus* ("*Mus chrysophilus*" and "*Mus decumans*"). The status of *Aethomys* as a genus is complicated, and Ellerman (1941) stated that "This genus is very difficult to classify, being one of the rather numerous African 'borderline' genera, overlapping to a certain extent *Rattus* on the one hand, and *Arvicanthis* on the other." Davis (1971) indicated that the content of the genus is still a matter for study, and some of the subgenera are a "mixed bag." Missone (1969) thought that *Aethomys* was "possibly an assemblage of different things."

Another cross reported by Gunning (1901) involved *Mus musculus* and *Rhabdomys pumilio.* He stated that "The result of a cross between the ordinary albino *Mus musculus* with the Striped Mouse (*Arvicanthis pumilio*) is a peculiarly cream-coloured, not striped specimen, which looks very much like a cream-albino Mouse with black eyes, which stand out very distinct against the cream-coloured fur." From what is known of the genetics of the coat color of *Mus*, it seems highly unlikely that the cream-colored animals would be the result of this cross, and before acceptance as a valid hybrid, confirmation is needed.

Gray (1972) also reported, on the basis of personal communication from E. Schlesser in 1952, a cross between *Rattus* (*Mastomys*) *natalensis*

and *Mus musculus*: "Seven hybrid young (3 ♂♂ and 4 ♀♀) have been reported. They were dark grey in colour, like R. *natalensis*. The hybrids showed remarkable growtn. They were wild like the father, and escaped before fertility could be ascertained." *Rattus natalensis* is currently placed in the genus *Praomys*, subgenus *Mastomys* (Missone 1969, 1971).

The distinction of *Rattus* and/or *Praomys* from *Mus* is based on characters of the tooth row. Ellerman (1941) pointed out that these do not hold up completely in separating *Rattus* and *Mus*. Missone's key (1971) pairs *Praomys* and *Mus* quite closely. Size alone will not distinguish *Rattus* and *Mus*, as there are species of the former that are smaller than some larger species of *Mus*. In the case of the supposed hybridization between *R. natalensis* and *Mus*, in the absence of any confirming data, because no one seems to have duplicated this cross, and in view of some question about Schlesser's report, as evinced by the following account, I prefer to defer acceptance of this cross until there are better data.

Also based on personal communication from Schlesser, Gray (1972) mentioned a cross believed to be between *Mus* (*Leggada*) sp. and *Mus musculus*: "In the Belgian Congo, a ♀ albino mouse produced offspring believed to be sired by a local wild mouse (*Leggada*)." *Leggada* is generally not recognized as more than a synonym of *Mus* (Ellerman, 1941; Missone, 1971).

Recommendation. Because of the content of the genera involved and even the parentage of the alleged hybrids is open to considerable question and requires further study and confirmation, no taxonomic allocations are recommended.

CETACEA

The intermediate characters of three dolphins stranded on the western coast of Ireland in 1933 led Fraser (1940) to suspect that they might be hybrids between *Tursiops truncatus* and *Grampus griseus*. He pointed out that both genera "are of equal size, about 12 feet, both have a common area of distribution and, so far as is known, the breeding times coincide. The bottle-nosed dolphin is known to be gregarious, and the effect of fertile hybridization would possibly be evident in succeeding generations to a varying extent, in different individuals within the school. There exists, however, no previous evidence of successful crossing between genera or even species of dolphins, although that fact in itself does not exclude the chance of its occurrence."

Fraser pointed out that, if the specimens he examined had not resulted from hybridization between *Tursiops* and *Grampus*, he might have considered "merging the two genera" because of the gradation in morphology. He rejected the idea that they were not intergrades because "they are so strikingly distinct that, in the present state of our knowledge, such a course would not be justified." Fraser considered and rejected the idea of naming the three specimens as new genera and species, although he found that under the criteria in use in taxonomy in 1940, one of the three specimens could represent a distinct species of *Tursiops* and the other two would rank as new genera.

At the time Fraser wrote, no other intergeneric hybrids, or even interspecific ones were known in the cetaceans. In 1974, however, Dohl, Norris, and Kang reported a viable hybrid from a female *Steno bredanensis* and a male *Tursiops truncatus*. *Steno* had been placed in the family Stenidae (Fraser, 1966) while *Tursiops* is in the family Delphinidae. Hershkovitz (1966) did not recognize the family Stenidae, although Rice (1967) did and suggested, on the basis of information from Fraser, that "it may be necessary to place each of these genera [*Sotalia*, *Sousa*, and *Steno*] in a separate family." However, by 1968, Rice and Scheffer had put *Steno* back into the Delphinidae. Mead (1975) on the other hand, kept *Steno* in the family Stenidae. Mead's anatomical studies of the nasal passages and facial complex of *Steno*, however, led him to point out that it was similar to *Tursiops*. He also noted the anatomical proximity of *Grampus* to *Tursiops*.

The generic synonymies for each of the hybrids and the earliest name according to priority are:

Tursiops Gervais, 1855 × *Grampus* Gray, 1828= *Grampus* Gray, 1828.

Tursiops Gervais, 1855 × *Steno* Gray, 1846= *Steno* Gray, 1846

Recommendation. Genus *Grampus* Gray, 1828, with *Steno* Gray, 1846, and *Tursiops* Gervais, 1855 as synonyms. Those who question the

recognition of the three specimens from the Irish coast (Fraser, 1940) as hybrids could recognize only the *Tursiops* × *Steno* hybrid, for which the earliest name is *Steno* Gray, 1846.

CARNIVORA

Among the carnivores there are a large number of intergeneric hybrids, some of which are widely known but are often disregarded as indications of taxonomic proximity.

In the family Canidae, hybridization between *Alopex lagopus* and *Vulpes vulpes* (including *Vulpes fulva*) is known and some F_1 offspring are fertile (Gray, 1972). Youngman (1975) used the combination *Vulpes lagopus* for Arctic foxes, concluding that they were congeneric, thus following Bobrinskii, Kuznetsov, and Kuzyakin (1944). Stains (1967) also had questioned the generic status of *Alopex* on the basis of its hybridization with *Vulpes*. Based on numerical classification analysis, Clutton-Brock, Corbet, and Hills (1976) maintained *Alopex* as a separate, monotypic genus, although they acknowledged that, in comparison with the other genera of canids they recognize, *Alopex* is "the least distinctive, and the skull and teeth show a very high degree of similarity to certain species of *Vulpes* especially *V. corsac*." Todd (1970), who analyzed canid phylogeny on the basis of karyotypes, stated that despite the distinctive chromosome complement of *Alopex*, "there appears to be no good reason beyond custom for sustaining such a [generic] distinction. All evidence, both morphological . . . and through hybridization studies . . . indicate a close relationship between *Alopex* and *V. vulpes*. Although hybrid sterility characterizes the products of this cross, the fact that a viable somatic animal is produced argues for no greater separation than specific."

Recognition of the genus *Thos* for jackals is generally not granted today, and in any event, hybridization between *Canis familiaris* as well as *Canis latrans* with jackals placed in the genus *Thos* have occurred with fertile offspring of both sexes produced.

Crosses of domestic dogs with other canids (and even with *Felis*) are often alleged, but many are questionable because adequate documentation on parentage is not given. Gray (1972) commented that hybridization between *Vulpes vulpes* and *Canis familiaris* had not been sustained; in one case that was checked cytologically, the offspring proved to be *C. familiaris*. Sanjeeva Raj (1953) reported hybrids from a female *Vulpes bengalensis* crossed with a domestic dog of Alsatian × bull-terrier parentage that was Dalmation in color. Photographs of the hybrids unfortunately do not help to substantiate this case.

In 1975 (Anon.) the birth of pups from a *Canis latrans* × *Vulpes vulpes* was reported at Bridgeton, New Jersey. Mr. Henry Ricci, Curator of the Cohanzick Zoo at Bridgeton, has kindly provided me with the details: A male coyote born April 5, 1971, was donated to the zoo in August of that year by a returning soldier. It was at first housed adjacent to a young female American red fox (*Vulpes vulpes*) that had been born about the same time as the coyote. Eight months later the two animals were put in the same cage and were compatible. During the first and second weeks of February 1973, the animals were seen to mate and on April 9, 1973, the vixen gave birth to two male pups. They were left with the female who began to ignore them on April 12. One was found dead that morning. The second pup was removed and hand fed, but died the evening of April 12 "probably due to congestion and exposure" according to Dr. Ernest Zirkle, the zoo's veterinarian.

Judging from photographs I have seen of the parents, there seems no reason to doubt their identification, nor does the appearance of the cage suggest entry by a local wild *Vulpes* male. The pups were preserved and are in the possession of Mr. Ricci and Dr. Zirkle.

According to their numerical analysis, Clutton-Brock, Corbet, and Hills (1976) found *Vulpes* and *Canis* to warrant generic separation on the morphological-numeric criteria of their study. They do point out, however, that determining the limits within the *Canis/Vulpes/Dusicyon* complex is difficult. "If *Dusicyon* were merged with *Canis*, it would be difficult to argue that *Vulpes* should not be treated likewise." Langguth (1975) did propose the inclusion of some of the South American canids generally known under the generic name *Dusicyon* in the genus *Canis*.

Krieg (1925) reported a hybrid between *Canis familiaris* and a pampas fox for which he used the name "*Pseudalopex* (*Canis*) *agarae*" [*sic*]. The specific name *azarae* has been used for at least eight taxa of South American canids, and it is difficult to ascertain which species actually may have been involved in the hybridization. Gray (1972) questionably assumed that *Cerdocyon thous* was the mother; there is equal likelihood that *Dusicyon gymnocercus* (=*culpaeus*?) may have been involved. According to Cabrera and Yepes (1940), there is anecdotal information that *Cerdocyon thous* X *Canis familiaris* hybrids were used by indigenous hunters in the Guianas. Although Langguth (1970, 1975) believed that *Cerdocyon* should be maintained as a distinct genus, Clutton-Brock, Corbet, and Hills (1976) regarded it as a member of an expanded genus *Dusicyon*. The arrangements of South American canids by Langguth in 1970 and 1975, and Clutton-Brock, Corbet, and Hills in 1976 are presented in table 1.

If Kreig's (1925) hybrid actually involved *Cerdocyon*, the logical conclusion would be a combination of Langguth's (1975) merging of *Dusicyon* with *Canis*, and Clutton-Brock, Corbet, and Hills's (1976) placement of *Cerdocyon* in *Dusicyon* with all in *Canis*. The proximity of *Dusicyon culpaeus* (including *culpaeolus*) to *Canis* (*adustus*, *mesomelas*, and *simensis*) is evident from Clutton-Brock, Corbet, and Hills, especially figures 4 and 5. Hershkovitz (1961) had also regarded *Cerdocyon* as being congeneric with *Dusicyon*.

Pocock (1941) mentioned a *Cuon* X *Canis aureus* cross in a Madras menagerie, but without further data, this hybrid is questioned.

No intergeneric hybrids in the family Procyonidae have been reported. In the family Mustelidae, the only report of an intergeneric hybrid is that of Ackermann (1898) cited by Gray (1972) between *Martes martes* and *Mustela putorius putorius*. However, adequate documentation for this is lacking, and considering that these are widely kept fur-bearers for which other crosses have been attempted, additional accounts would be expected to have been reported.

Based on the hybridization of some of the Ursidae reported by Gray (1972) the status of most of the genera seems open to question. The polar bear, formerly considered *Thalarctos*, has been shown to be capable of crossing with *Ursus arctos* and the offspring are fertile. The American black bear, formerly considered the genus *Euarctos* and still sometimes placed in its own subgenus, has produced viable offspring when crossed with *Ursus arctos*. One such hybrid was successfully backcrossed to a grizzly bear (*U. a. horribilis*). *Ursus arctos* has also been crossed with *Selenarctos thibetanus* and produced a viable off-

TABLE 1
Comparison of Three Classifications of South American Canids

Clutton-Brock, Corbet, and Hills, 1976	Langguth, 1975	Langguth, 1970
Vulpes cinereoargenteus	*Urocyon cinereoargenteus*	*Urocyon cinereoargenteus*
Dusicyon australis	*Canis (Dusicyon) australis*	*Dusicyon (Dusicyon) australis*
Dusicyon culpaeus	*Canis (Pseudalopex) culpaeus*	*Dusicyon (Pseudalopex) culpaeus*
Dusicyon culpaeolus		[= *D. culpaeus andensis*]
Dusicyon gymnocercus	*Canis (Pseudalopex) gymnocercus*	*Dusicyon (Pseudalopex) gymnocercus*
Dusicyon inca		[= *D. culpaeus andensis*]
Dusicyon griseus	*Canis (Pseudalopex) griseus*	*Dusicyon (Pseudalopex) griseus*
Dusicyon fulvipes		[= *D. griseus fulvipes*]
Dusicyon sechurae	*Canis (Pseudalopex) sechurae*	*Dusicyon (Pseudalopex) sechurae*
Dusicyon vetulus	*Lycalopex vetulus*	*Lycalopex vetulus*
Dusicyon thous	*Cerdocyon thous*	*Cerdocyon (Cerdocyon) thous*
Dusicyon microtis	*Atelocynus microtis*	*Cerdocyon (Atelocynus) microtis*
Chrysocyon brachyurus	*Chrysocyon brachyurus*	*Chrysocyon brachyurus*
Speothos venaticus	*Speothos venaticus*	*Cerdocyon (Speothos) venaticus*

spring (Gray, 1972; Duplaix-Hall, 1975). Asakura (1969) reported mating of *Helarctos malayanus* with *Melursus ursinus* and the birth of a single cub 95 days later. Thus of the six genera of bears that were recognized by Simpson in 1945, only one, *Tremarctos*, has not been known to hybridize with some other genus of bear:

Ursus × *Thalarctos*
× *Selenarctos*
Helarctos × *Melursus*

Simpson (1961) acknowledged that the hybridization between *Thalarctos* and *Ursus* indicated congeneracy. However, the generic name *Thalarctos* is still widely used for the polar bear, especially in Europe. The validity of *Selenarctos* as a genus was also questioned by Ellerman and Morrison-Scott (1951). Bobrinskii, Kuznetsov, and Kuzyakin (1944) referred both *Selenarctos* and *Thalarctos* to *Ursus*. The record of a hybrid between *Melursus* and *Helarctos* also points to the genetic proximity of these bears. Simpson (1945) stated that all of the nominal genera of living bears were "very closely allied." Thenius (1976) found *Tremarctos* to be subfamilialy distinct from the other living bears.

There are no intergeneric crosses reported from the viverrids or the hyaenids.

The felids have, at times, been placed in many genera and subgenera, very nearly one for each species. Current usage is still variable, and ranges from recognition of only two genera, *Acinonyx* for the cheetah and *Felis* for all other living cats, to finer distinctions, the most common being the consideration that, in addition to the cheetah as a distinct genus, *Felis* be split into the "large" cats under the name *Panthera* or *Leo* and the "small" cats with *Felis* as the generic name. *Neofelis* is often distinguished generically as well, and recognition of the snow leopard as *Uncia* and the lynxes as *Lynx* is not uncommon. Simpson (1945) listed three genera: *Acinonyx*, *Panthera* (with six subgenera, one for each species), and *Felis* (with 16 possible subgenera for about 29 species).

Hybridization (Gray, 1972) between lions (subgenus *Leo*) and tigers (subgenus *Tigris*), lions and leopards (subgenus *Panthera*), lions and jaguars (subgenus *Jaguarius*), between tigers and leopards, and between jaguars and leopards has been accomplished. Some of the offspring are fertile in these crosses, and the ability to hybridize bespeaks the genetic proximity of these species and questions their separation into genera or even subgenera. The hybridization of *Felis catus* with *Lynx rufa* (Gray, 1972) similarly creates doubt as to the generic separability of the nominal genus *Lynx*.

Of more taxonomic importance is the hybridization of *Panthera pardus* with *Felis concolor* reported in Gray (1972). The production of viable offspring from this cross implies that *Panthera* and *Felis* are congeneric or that *Felis concolor* should be placed in *Panthera*—a consideration that would be regarded as unacceptable on the morphological grounds that are supposed to distinguish *Panthera*.

I have used the name *Panthera* for the "large" cats here because that is the name that Gray (1972) used; however, the nomenclature is currently *sub judice* (and presumably has been for a quarter of a century) by the International Commission for Zoological Nomenclature. As previously expressed (Van Gelder, 1975), my belief that the correct name for the large cats, if one is to be used at all, is *Leo*.

In the pinnipeds, hybridization has occurred between *Arctocephalus pusillus* and *Zalophus californianus* (Gray, 1972). These two genera are sometimes placed in separate subfamilies (Stains, 1967), which classification the hybridization would question. Another hybrid between *Zalophus* and some other otariid, either *Arctocephalus pusillus* or *Otaria byronii*, has also been reported (Gray, 1972). The most parsimonious consideration would be to regard it as a *Zalophus* × *Arctocephalus* cross, even though the zookeepers suspected *Otaria* as the sire. The alleged hybridization between *Callorhinus ursinus* and *Otaria byronii* which Gray (1972) cited from Ackermann (1898) does not seem likely on the geographic grounds of its basis and may represent an error in updating synonymy. The statement in Ackermann is based on an observation attributed to Steller, and might refer to *Eumetopias*, rather than *Otaria*, and *Callorhinus*. However, it would require further substantiation before I accept it.

In the phocids, a newborn but dead hybrid between *Halichoerus grypus* and *Phoca hispida*

was found in the Stockholm zoo in 1929 (Gray, 1972).

Simpson (1945) recognized five genera of otariids (*Arctocephalus*, *Callorhinus*, *Zalophus*, *Eumetopias*, and *Otaria*). Scheffer (1958) separated *Neophoca* from *Zalophus* as an additional genus. Winge (1941), however, had a much broader view, recognizing only *Arctocephalus* and *Otaria* in what is usually considered the family Otariidae.

The generic synonymies for each of the carnivoran hybrids accepted as valid by me, and the earliest name according to priority are:

Alopex Kaup, 1829 × *Vulpes* Bowdich, 1821= *Vulpes* Bowdich, 1821.

Vulpes Bowdich, 1821 × *Canis* Linnaeus, 1758= *Canis* Linnaeus, 1758.

Dusicyon H. Smith, 1839 × *Canis* Linnaeus, 1758=*Canis* Linnaeus 1758.

Thalarctos Gray, 1825 × *Ursus* Linnaeus, 1758= *Ursus* Linnaeus, 1758.

Selenarctos Heude, 1901 × *Ursus* Linnaeus, 1758=*Ursus* Linnaeus, 1758.

Helarctos Horsfield, 1825 × *Melursus* Meyer, 1793=*Melursus* Meyer, 1793.

Panthera Oken, 1816 × *Felis* Linnaeus, 1758= *Felis* Linnaeus, 1758.

Zalophus Gill, 1866 × *Arctocephalus* E. Geoffroy St.-Hilaire and F. Cuvier, 1826=*Arctocephalus* E. Geoffroy St.-Hilaire and F. Cuvier, 1826.

Recommendation. Canis Linnaeus, 1758, including *Alopex* Kaup, 1829, *Urocyon* Baird, 1857, *Fennecus* Desmarest, 1804, *Vulpes* Bowdich, 1921, *Cerdocyon* Hamilton-Smith, 1839, and *Dusicyon* Hamilton Smith, 1839. This recommendation represents a combination of taxonomic conclusions mainly by Langguth (1970, 1975) and Clutton-Brock, Corbet, and Hills (1976) and the data from hybridization. The latter recognized the genus *Vulpes* to include *Urocyon* and *Fennecus*, to which may be added *Alopex* on the basis of its hybridization with *Vulpes*. Langguth (1975) concluded that *Dusicyon* (species *australis*, *griseus*, *sechurae*, and *culpaeus*) was more properly placed within the genus *Canis*, but continued to recognize *Cerdocyon*. Clutton-Brock, Corbet, and Hills (1976) included *Cerdocyon* in *Dusicyon*. The present recommendation of a broadly construed genus *Canis* seems to represent a balanced appraisal of the genus from the separate conclusions of the authorities, Langguth, Clutton-Brock, Corbet, and Hills, together with the genetic information provided by the known hybridizations.

Ursus Linnaeus, 1758, with *Thalarctos* Gray, 1825 and *Selenarctos* Heude, 1901 as synonyms.

Melursus Meyer, 1793 with *Helarctos* Horsfield, 1825 as a synonym.

Felis Linnaeus, 1758 with *Panthera* Oken, 1816 (=*Leo* Brehm, 1829) as a synonym.

Arctocephalus E. Geoffroy St.-Hilaire and F. Cuvier, 1826 with *Zalophus* Gill, 1866 as a synonym.

PERISSODACTYLA

Other than in the family Equidae, no hybrids are reported for the perissodactyls. Each of the seven species of generally recognized equids has been shown to be capable of hybridizing with virtually each of the other species with which mating has been attempted. The offspring are almost always sterile. Various subgenera have been suggested for many of the species, and sometimes have been used as genera (*Asinus*, *Hippotragus*, *Dolichohippus*, *Onager*, *Hemionus*). The hybridization data would suggest that these taxonomic categories are questionable at the generic level.

ARTIODACTYLA

No intergeneric hybrids are reported from the families Suidae, Hippopotamidae, Camelidae, Tragulidae, or Giraffidae.

In the family Tayassuidae, there are three living species, the third being the newly discovered South American *Catagonus*, a genus formerly known only from fossils (Wetzel et al., 1975). Simpson (1945) recognized *Catagonus*, which he knew only as a fossil, and put the other two living peccaries in the single genus *Tayassu*. Woodburne (1968) concluded that the two living species of peccaries then known were generically distinct, with *Tayassu pecari* for the white-lipped and *Dicotyles tajacu* for the collared peccary. The generic distinction of these two peccaries was initially followed by Wetzel et al. (1975), but later Wetzel (1976) indicated that he considered *Tayassu* and *Dicotyles* congeneric. This

conclusion would seem to be in keeping with the information (Gray, 1972) that *Tayassu* and *Pecari* (=*Dicotyles*) had successfully been hybridized at the London Zoo.

In the family Cervidae, the number of genera has been reduced since 1945 when Simpson listed 17. His arrangement included a number of suprageneric divisions, and no subgeneric ones. Comparison of Simpson's (1945) arrangement with that of Haltenorth (1963) is given below.

The 17 genera of Simpson are arranged by Haltenorth in 11 genera, all of the generic lumping taking place within Simpson's subfamilies Cervinae and Odocoileinae. The data available from intergeneric hybridizations not only bear out Haltenorth's conclusions, but suggest additional generic lumping.

On the basis of hybridization, it would appear that the subfamily Cervinae, as construed by Simpson (1945) with *Dama*, *Axis*, *Cervus*, and *Elaphurus*, would comprise only a single genus, *Cervus*. Except for *Elaphurus*, Haltenorth (1963) included all of these in *Cervus*, recognizing *Dama* and *Axis* as subgenera, as well as a number of other subgenera. Hybridization between *Cervus elaphus* and *Elaphurus davidianus* has been reported (Gray, 1972), and fertile young of both sexes have been backcrossed to *C. elaphus*. Crosses between a number of the nominal subgenera (see Gray, 1972) are known.

Two reported hybridizations involving *Cervus* (as construed by Haltenorth, 1963) would seem to bear on higher categories of the deer. Simpson (1945) considered a major division to be between the Cervinae and the Odocoileinae. He put *Capreolus* in its own tribe, Capreolini, in the Odocoileinae. Haltenorth, too, allied *Capreolus* with the Odocoilinae [*sic*], and in a sense placed them even closer to *Odocoileus* in that he did not erect a subfamily for *Capreolus*, as he did for

Simpson, 1945	Haltenorth, 1963
Family Cervidae	Family Cervidae
Subfamily Moschinae	Subfamily Moschinae
Genus *Moschus*	Genus *Moschus*
Subfamily Muntiacinae	Subfamily Munticinae
Tribe Muntiacini	
Genus *Muntiacus*	Genus *Muntiacus*
Genus *Elaphodus*	Genus *Elaphodus*
Subfamily Cervinae	Subfamily Cervinae
Genus *Dama*	Subgenus *Dama*, Genus *Cervus*
Genus *Axis*	Subgenus *Axis*, Genus *Cervus*
Genus *Cervus*	Genus *Cervus*, Subgenus *Cervus*
Genus *Elaphurus*	Genus *Elaphurus*
Subfamily Odocoileinae	Subfamily Odocoilinae
Tribe Odocoileini	
Genus *Odocoileus*	Genus *Odocoileus*
Genus *Mazama*	Genus *Mazama*
Genus *Hippocamelus*	Subgenus *Hippocamelus*, Genus *Odocoileus*
Genus *Blastocerus*	Subgenus *Odocoileus*, Genus *Odocoileus*
Genus *Ozotoceras*	Subgenus *Blastoceros*, Genus *Odocoileus*
Genus *Pudu*	Subgenus *Pudu*, Genus *Mazama*
Tribe Alcini	Subfamily Alcinae
Genus *Alces*	Genus *Alces*
Tribe Rangiferini	Subfamily Rangiferinae
Genus *Rangifer*	Genus *Rangifer*
Tribe Hydropotini	Subfamily Hydropotinae
Genus *Hydropotes*	Genus *Hydropotes*
Tribe Capreolini	
Genus *Capreolus*	Genus *Capreolus*, Subfamily Odocoilinae

each of Simpson's other tribes in this group. Both *Capreolus* and *Odocoileus* were reputed (Gray, 1972) to have hybridized with species now included in the genus *Cervus*, and in the subfamily Cervinae of Simpson (1945).

Gray (1972) reported two instances of hybridization of *Axis* with *Odocoileus*. One of these, *Axis axis* × *Odocoileus virginianus*, she cited from Lantz (1910). Lantz (1910) stated merely that "the chital or spotted deer (*Cervus axis*) of India and Ceylon . . . has been crossed with the Virginia deer." Subsequently, he attributed this information to Caton (1877). If Caton's stock actually did come from Ceylon, the animals involved in the hybridization could have been either *Axis* (*Hyelaphus*) *porcinus* or *Axis axis ceylonensis*. From Caton's descriptions, it is not possible to distinguish the two, nor is it possible to avoid the conclusion that his "Ceylon deer" and "Acapulco deer" (which have been regarded as *Odocoileus virginianus*) were actually the same species. Again and again Caton indicated how similar the two were in antlers, coloration, tail, and other characters. Inasmuch as it does not seem possible to determine accurately what species may have been involved in these crosses, I deem it best to regard these data as too dubious for consideration. What seems to be a second account of an *Axis* × *Odocoileus* cross in Gray (1972) is cited from Przibram (1910) whose information is derived also from Caton (1877).

Gray (1972) cited a reference to the hybridization of *Capreolus capreolus* with *Axis* (*Hyelaphus*) *porcinus*. She derived her data from Rörig (1903) who reported that two hybrids were born at the Dresden Zoological Garden in May 1862. The fawns, one of each sex, lived only for eight days. Rörig gave as his reference "Z. [oologische] G.[arten] 2.65", but no reference to this cross appears there, nor does there seem to be any such account from the Dresden Zoological Garden within a year or two of that time. If this case of hybridization actually involved the two genera as stated, then a question of the alliance of *Capreolus* with the Odocoileines would be raised. Flerov (1952), incidentally, allied *Capreolus* with *Cervus* (with *Rusa*, *Axis*, and *Dama* as subgenera), *Alces*, and *Elaphurus* as members of his subfamily Cervinae. However, until substantiation of *Capreolus* × *Axis* (=*Cervus*) hybridization is made, it is best to regard the record as questionable. Gray's other citation of a *Capreolus* cross, an interfamilial one with *Ovis aries*, is not regarded as valid.

The alleged hybrid between *Alces* and *Cervus canadensis* (Gray, 1972; Anon., 1931) is undocumented by a specimen and is not regarded as valid. Of even greater doubt is a reputed interfamilial *Alces* × *Bos taurus* cross (Gray, 1972).

The higher categories of the family Bovidae have received varied treatments. Simpson (1945) arranged them in five subfamilies: Bovinae, Cephalophinae, Hippotraginae, Antilopinae, and Caprinae, and split these into tribes. Haltenorth (1963) put the bovids into 10 subfamilies with 22 tribes, and reduced the number of genera from Simpson's 54 to 42 by the inclusion of *Bibos* in *Bos*, and *Anoa* and *Synceros* in *Bubalus*, *Philantomba* and *Sylvicapra* in *Cephalophus*, *Gorgon* in *Connochaetes*, *Beatragus* in *Damaliscus*, *Adenota* and *Onotragus* in *Kobus*, *Rhynchotragus* in *Madoqua*, *Nesotragus* in *Neotragus*, and *Taurotragus* in *Tragelaphus*. Haltenorth considered *Tragelaphus* De Blainville, 1816 as the appropriate name for what Simpson called *Strepsiceros* Frisch, 1775. Koopman's (1967) arrangement of Simpson's five families was essentially that of Simpson, but he followed Haltenorth except for retaining *Sylvicapra* and *Taurotragus* as valid genera.

The data from hybridization confirm some of Haltenorth's generic amalgamations. The banteng (*Bibos banteng*) and the gaur and gayal (*Bibos frontalis* and/or *gaurus*) not only hybridize with one another in captivity, but also with members of the genus *Bos* including *B. indicus*, *B. taurus*, and *B.* (*Poephagus*) *grunniens*. Some degree of fertility exists in some offspring of these crosses. Haltenorth (1963) recognized *Bibos* as a subgenus of *Bos*, with two species, *B. javanicus* (the banteng) and *B. gaurus* (the gaur).

The genus *Bison* of Simpson (1945) and Haltenorth (1963) is also capable of hybridizing with the "genus" *Bibos*, as an offspring resulted from a cross between a *Bison* bull and a female *Bos indicus* × *Bibos gaurus* hybrid. This triple hybrid was also fertile when backcrossed to *Bison* (Gray, 1972). *Bison* has also been successfully crossed with another hybrid, *Bos* (*Poephagus*) *grunniens* × *Bibos frontalis* (Gray,

1972). Fertile offspring have resulted from crosses of *Bison* with *Bos indicus* as well as with *Bos taurus*. Haltenorth (1963) considered *Bison bison* and *Bison bonasus* to be conspecific, and listed them under the latter name. Hybrids between these two nominal species are fertile in both sexes.

Gray (1972) listed a number of crosses involving *Bos taurus* and/or *B. indicus* with *Alces*, *Bubalus*, *Cervus*, *Ovibus*, *Ovis*, and *Taurotragus*. None of these is believed to have been successful in producing offspring.

Haltenorth (1963) included *Taurotragus* and *Boocercus* in the genus *Tragelaphus*, regarding them both as belonging to the subgenus *Taurotragus*. Koopman (1967) did not follow Haltenorth in this, leaving *Taurotragus* as a genus. Ansell (1971) regarded *Boocercus* as only a subgenus within *Tragelaphus*, largely on the basis of the hybridization of *Boocercus eurycerus* with *Tragelaphus spekei* (Tijskens, 1968), but in regard to a *Taurotragus oryx* × *Tragelaphus strepsiceros* hybrid (Bolineau, 1933), Ansell required knowledge of the fertility of the hybrid before making a generic change. I have commented elsewhere (Van Gelder, 1977) on this cross, and it has recently been repeated at the San Diego Zoo (Jorge, Butler and Benirschke, 1976). Female hybrids of the *Boocercus* × *Tragelaphus spekei* cross were fertile (Koulischer, Tijskens and Mortelmans, 1973). *Taurotragus oryx* has also been successfully crossed with *Tragelaphus spekei* (Anon, 1975).

Neither Koopman (1967) nor Ansell (1971) followed Haltenorth's (1963) inclusion of *Sylvicapra* in *Cephalophus*. They did include the third genus of duiker that Simpson recognized in the subfamily Cephalophinae, *Philantomba*, as a synonym of *Cephalophus*. *Sylvicapra*, however, has hybridized with *Cephalophus nigrifrons* (Anon., 1965). Another hybrid (Bigalke, 1932) died shortly after birth and had an abnormal lower jaw. The presumptive parents of this cross were *Sylvicapra grimmia* and *Cephalophus natalensis*. Lydekker and Blaine (1914) had earlier considered *Sylvicapra* and *Cephalophus* as congeneric.

Simpson (1945) recognized five genera in his tribe Alcelaphini: three hartebeests, *Damaliscus*, *Alcelaphus*, and *Beatragus*; and two wildebeests, *Connochaetes* and *Gorgon*. Haltenorth (1963) divided this group into two tribes, Alcelaphini with *Damaliscus* and *Alcelaphus*, regarding *Beatragus hunteri* as no more than a subspecies of *Damaliscus lunatus*, and Connochaetini with a single genus, *Connochaetes*, divided into subgenera *Connochaetes* and *Gorgon*. Koopman (1967) followed this generic arrangement, but recognized three species in *Damaliscus*, evidently considering *hunteri* a valid species. Ansell (1971) likewise recognized *hunteri*, *dorcas*, and *lunatus* as the species of *Damaliscus*. Although Haltenorth (1963) recognized only a single species of *Alcelaphus*, Koopman (1967) and Ansell (1971) both recognized two species, *A. buselaphus* and *A. lichtensteini*.

Hybridization between the red hartebeest, *Alcelaphus buselaphus*, and the blesbok, *Damaliscus dorcas phillipsi*, was reported by Kettlitz (1967). Although these hybrids were presumably sterile, they had grown to maturity. Selous (1893) reported on a specimen that was thought to be a hybrid between the red hartebeest (*A. buselaphus caama*) and the tsessebe (*Damaliscus lunatus lunatus*).

Gorgon as a genus for the black wildebeest is usually not recognized today, although some regard it as a valid subgenus. Viable and fertile hybrids have been produced between the black wildebeest and blue (*Connochaetes taurinus*) according to documentation in Ansell (1971).

In 1945 Simpson recognized five genera in his tribe Reduncini: *Kobus*, *Adenota*, *Onotragus*, *Redunca*, and *Pelea*. Haltenorth (1963) put *Pelea* in its own tribe, Peleini, while Ansell (1971) raised it to subfamilial rank, Peleinae. Ansell (1971) and Haltenorth (1963) retained *Redunca* as a genus in the subfamily Reduncinae (Ansell) or tribe Reduncini (Haltenorth) along with the single genus *Kobus*. Haltenorth (1963) recognized four species of *Kobus*, each of which he put in its own subgenus: *K.* (*Kobus*) *ellipsiprymnus*, including *defassa*; *K.* (*Adenota*) *kob*, including *vardoni*; *K.* (*Hydrotragus*) *leche*; and *K.* (*Onototragus*) *megaceros*. Ansell (1971) did not recognize any subgenera of *Kobus*, and considered *K. vardoni* a valid species. Of Simpson's genera and Haltenorth's subgenera, Gray (1972) recorded hybrids between *Kobus* and *Adenota*,

Kobus and *Onototragus*, and *Hydrotragus* and *Onototragus*. A fertile hybrid of a *Kobus* × *Onototragus* cross was successfully mated with an *Adenota*. Ansell (1971) pointed out that Haltenorth's use of the name *Onototragus* Heller, 1913, for *K. megaceros* was an error; Heller's name was an erroneous spelling of *Onotragus*, for which the type is *K. leche*. *Hydrotragus* Fitzinger (1866) may be an earlier name for *Onotragus* (Ellerman, Morrison-Scott and Hayman, 1953).

Simpson (1945) erected the tribe Caprini for five genera: *Ammotragus*, *Capra*, and *Ovis*, *Hemitragus*, and *Pseudois*. Haltenorth (1963) followed this classification. Ansell (1971) who was concerned only with African genera, pointed out that *Ammotragus* had not only been hybridized with domestic *Capra hircus*, but that the offspring were fertile when backcrossed with a male *Capra ibex*. This led Ansell to regard *Ammotragus* as a subgenus of *Capra*, as *Capra* (*Ammotragus*) *lervia*. Attempted hybridization between *Ammotragus* and *Ovis aries* either from natural (captive) matings or artificial insemination was not successful in producing an offspring (Gray, 1972). Nadler, Hoffmann and Wolf (1974), on the basis of chromosomal homologies, postulated that *Ammotragus* was closer to the ancestral lineage of *Ovis* than to *Capra*. Manwell and Baker (1975), however, found that biochemical analyses of sheep, goat, and aoudad haemoglobins "suggest that *A. lervia* is no closer to *Ovis* than to *Capra*; indeed, the nature of the α chain duplication indicates that there is more in common between *A. lervia* and *C. hircus* than between *A. lervia* and *O. aries*."

Hybrids between goats (*Capra*) and sheep (*Ovis*) have long been reported, but seldom adequately documented. Between the time of Gray's 1954 compilation and that of 1972, hybridization between *Capra hircus* and *Ovis aries* with the production of viable offspring that were fertile when artificially inseminated with *Ovis* semen was reported (see Gray, 1972, for extensive bibliography). An additional instance of hybridization between *Ovis aries* and *Capra ibex* was believed to have involved *C. hircus*, rather than *C. ibex*. *Capra hircus* and *C. ibex* are interfertile, in any event (Gray, 1972).

The similarities of sheep and goats have long been noted, and the amount of reliance on external characteristics required to differentiate them is well indicated by Ellerman and Morrison-Scott's (1951) table of differences.

The generic synonymies for each of the artiodactyl intergeneric hybrids I deem valid, and the earliest name according to priority are:

Tayassu Fischer, 1814 × *Pecari* Reichenbach, 1835 or *Dicotyles* Cuvier, 1817=*Tayassu* Fischer, 1814.

Dama Frisch, 1775 (invalid) or *Platyceros* Zimmermann, 1780 × *Axis* Smith, 1827=*Platyceros* Zimmermann, 1780.

Axis H. Smith, 1827 × *Cervus* Linnaeus, 1758=*Cervus* Linnaeus, 1758.

Elaphurus Milne-Edwards, 1866 × *Cervus* Linnaeus, 1758=*Cervus* Linnaeus, 1758.

Bibos Hodgson, 1837 × *Bos* Linnaeus, 1758=*Bos* Linnaeus, 1758.

Bison H. Smith, 1827 × *Bos* Linnaeus, 1758=*Bos* Linnaeus, 1758.

Taurotragus Wagner, 1855 × *Tragelaphus* De Blainville, 1816=*Tragelaphus* De Blainville, 1816.

Boocercus Thomas 1902 × *Tragelaphus* De Blainville, 1816=*Tragelaphus* De Blainville, 1816.

Sylvicapra Ogilby, 1837 ×*Cephalophus* H. Smith, 1827=*Cephalophus* H. Smith, 1827.

Damaliscus Sclater and Thomas, 1894 × *Alcelaphus* De Blainville, 1816=*Alcelaphus* De Blainville, 1816.

Gorgon Gray, 1850 × *Connochaetes* Lichtenstein, 1814=*Connochaetes* Lichtenstein, 1814.

Adenota Gray, 1847 × *Kobus* A. Smith, 1840=*Kobus* A. Smith, 1840.

Onotragus Gray, 1872 (=*Hydrotragus* Fitzinger, 1866) × *Onototragus Haltenorth*, 1963 (*nec* Heller, 1913)=*Hydrotragus* Fitzinger, 1866.

Onototragus Haltenorth, 1963 (*nec* Heller, 1913) × *Kobus* A. Smith, 1840=*Kobus* A. Smith, 1850.

Ammotragus Blyth, 1840 × *Capra* Linnaeus, 1758=*Capra* Linnaeus, 1758.

Ovis Linnaeus, 1759 × *Capra* Linnaeus, 1758=*Capra* Linnaeus, 1758 (page priority).

Recommendation. *Tayassu* Fischer, 1814, with *Dicotyles* Cuvier, 1817, and its synonym *Pecari* Reichenbach, 1835, as synonyms.

Cervus Linnaeus, 1758, with *Dama* Frisch, 1775 (=*Platyceros* Zimmermann, 1780), *Axis* H. Smith, 1827, and *Elaphurus* Milne Edwards, 1866, as generic synonyms.

Bos Linnaeus, 1758, with *Bibos* Hodgson, 1837, and *Bison* H. Smith, 1817, as synonyms.

Tragelaphus De Blainville, 1816, with *Taurotragus* Wagner, 1855, and *Boocercus* Thomas, 1902, as synonyms.

Cephalophus H. Smith, 1827, with *Sylvicapra* Ogilby, 1837, as a synonym.

Alcelaphus De Blainville, 1816 with *Damaliscus* Sclater and Thomas, 1894, and *Beatragus* Heller, 1912 (following Haltenorth, 1963, and Ansell, 1971) as generic synonyms.

Connochaetes Lichtenstein, 1814, with *Gorgon* Gray, 1850, as a synonym.

Kobus A. Smith, 1840, with *Adenota* Gray, 1847, and *Onotragus* Gray, 1872 (=*Hydrotragus* Fitzinger, 1866) as synonyms.

Capra Linnaeus, 1758, with *Ovis* Linnaeus, 1758, and *Ammotragus* Blyth, 1840, as synonyms.

DISCUSSION AND CONCLUSIONS

A trend in taxonomy for more than a century has been to increase the objectivity by which taxa are distinguished. For the most part this trend has been concerned with the species and infraspecies categories. The utilization of a broader spectrum of data than morphology alone—the "new systematics" and the application of reproductive compatibility or incompatibility to the definition and concept of the species—has been a major component in an objective approach to taxonomy. In addition, the establishment of statistical and population parameters for species and subspecies, and the utilization of computers to group data and taxa are further indications of this trend. The attempt to apply objective criteria to taxonomic categories higher than species is quite recent, stemming in part from the clustering evaluations that can be produced by computers. Cladistic analysis, similarly, is another approach to attempt to reduce the subjectivity of the investigator and is applied primarily to taxonomic categories higher than species. All of these techniques, however, have strong subjective components, as the selection of criteria for analysis or the evaluation of primitive and advanced, or what is shared, are still products of the investigator's personal and scientific objectives.

The application of reproductive data to higher categories, as proposed here, has largely been ignored. In part, perhaps, this stems from the concept that the criterion of reproductive isolation for the species is unspokenly accepted as a component of the definition of the genus and higher categories. When investigators have faced the question of intergeneric hybridization of mammals, they have usually concluded that the production of a viable offspring from supposedly different genera is or might be sufficient grounds for lumping the genera (Buettner-Janusch, 1966; Simpson, 1961; Stains, 1967; Ansell, 1971; Van Gelder, 1977). To my knowledge, the present paper is the first attempt to consider all known intergeneric mammals in hybrids in the context of the validity of the genera and to apply the concept of reproductive incompatibility to the definition of the genus.

Basically, the logic of a reproductively isolated and self-contained genus seems inescapable if one accepts the *concept* of the reproductively isolated species. The genus neither can nor should be of less dimension than the species, and if the parameters of the species are ultimately established by its reproductive capabilities, then the genus, too, must be so proscribed. The greatest extent of reproductive compatibility allowed between species is generally the production of sterile offspring. The production of fertile offspring in nature is usually sufficient grounds for merging the parental stocks into a single species with their recognition only as subspecies. Similarly, for allopatric species, captive hybridization with fertile offspring may be used to consider the parental stocks conspecific. If these are the reproductive limits of species it would seem to follow that the genus must be reproductively at least, if not more, separable, and that crosses between genera be wholly incapable of producing a live offspring.

The utilization of reproductive data in defining genera, especially as applied in this paper, is open to a number of criticisms. In some cases,

especially older ones, the identity of the genera involved in the cross may be erroneous, or the parentage of the hybrid may somehow be suspect. Although I have tried to eliminate those that I or others (e.g., Gray, 1972) viewed with reservation, some of the data remaining may still be erroneous, leading to incorrect taxonomic conclusions.

No systematic attempts at hybridization for the purpose of determining generic status have been made. Most of the data are the result of fortuitous matings in zoos or laboratories. As a result, the data for any group of mammals are not uniform, and while there may be evidence that species of genera A and B may hybridize, the status of species in genus C in, for example, the same tribe or subfamily may not be resolved. Objection to the use of hybridization data on these grounds is the same as has been raised by some (e.g., Blackwelder, 1967) against the use of the "biological" species concept. However, to ignore data when they exist by demanding equivalent data for all taxa seems not only grossly unscientific, but if applied uniformly would stultify taxonomy and science as a whole.

For the most part, the genus has been accepted and utilized as an arbitrary category. Mayr, Linsley and Usinger (1953) stated "An objective criterion for generic rank does not exist equivalent, let us say to reproductive isolation as a species criterion. It is therefore impossible to give an objective definition of the genus." Although they did not deal with reproductive compatibility between genera, Mayr, Linsley and Usinger (1953), who recognized and fostered the "biologic species' concept, tied the genus firmly to the species in their definition" "*A genus is a systematic category including one species or a group of species of presumably common phylogenetic origin, which is separated from other similar units by a decided gap.*" (Italics theirs.) They regarded the species as having the essential property of reproductive isolation, while they clearly indicate that the essence of the genus is morphological distinctness. They did not deal with the lower limits of the genus to consider what happens at the interface between the criteria of reproductive isolation with morphologic distinctness. However, since their definition of the genus incorporates the concept of the reproductively isolated species, one must assume that reproductive isolation is also a component of the definition of a genus.

That Mayr, Linsley and Usinger (1953) and others (e.g., Ross, 1975) regard the genus as arbitrary is evident in their guidelines for the size of genera, essentially "lumping" monotypic species and "splitting" large genera. Ross (1975) stated his contention that a genus should not contain more than 40 species. These suggestions contain the premise that the genus is not a "real" evolutionary component but only a human artifact developed for convenience in handling species. Schaefer (1976) discussed the "reality" of higher categories from an evolutionary viewpoint of adaptive levels.

The generic groupings proposed in this paper unintentionally fit within the criteria of Ross for genera. The broadly construed genus *Cercopithecus* contains exactly 40 species; the most species the genus *Canis* would have is 36; and all other genera would have fewer. The idea of an arbitrary 40 as the limit on the size of a genus is neither biological nor evolutionary, and not even representative of convenience. As of 1967 (data from Anderson and Jones, 1967, except as noted) there were 12 genera (about 1% of the genera of living mammals) with 40 or more species: *Crocidura*, 160; *Sorex*, 40; *Pteropus*, 65; *Rhinolophus*, 71 (reduced to 68 in Koopman and Jones, 1970); *Hipposideros*, 43 (increased to 44 in Koopman and Jones, 1970); *Myotis*, 68; *Pipistrellus*, 50; *Tadarida*, 49 (reduced to 45 in Koopman and Jones, 1970); *Oryzomys*, 58; *Peromyscus*, 57; *Microtus*, 58; and *Rattus*, 120. Thus, some 20 percent of the species of living mammals are considered to exist in genera that would be regarded by Ross (1975) as too large.

A criticism of the generic groupings proposed here is that there would be a loss of the "information content" of the genera. Presumably this implies an intellectual concurrence of the extent of a particular genus, a contention that lacks merit either in theory or in practice. If the genus is arbitrary, then the use of a generic name has information content no greater than that of the species that is the type of the genus. If one talks of the genus *Peromyscus*, does that automatically

include or exclude *Baiomys* or *Ochrotomys*? does a discussion of *Papio* include *Mandrillus*, or does mention of *Macaca* include *Cynopithecus*? Because the category of genus is flexible and somewhat arbitrary and therefore subject to varied interpretation, its ability to convey information concerning its content is fundamentally limited. The application of reproductive data, as proposed in this paper should, in fact, serve to reduce the arbitrariness of the concept of the genus and thereby enhance the stability of its information content.

The idea of a stable genus with a fixed information content exists largely only as an element of taxonomic tradition and experience, and in practice one finds constant fluctuation. In the 14 years between the publication of Allen's checklist of African mammals (1939) and that of Ellerman, Morrison-Scott and Hayman for southern Africa (1953), 51 of 210 (24%) generic names of mammals from southern Africa were changed, three for nomenclatural reasons, the remainder on taxonomic grounds (Van Gelder, 1975). In the 22 years from the publication of Simpson (1945) to that of Anderson and Jones (1967) the number of Recent genera increased from 932 to 1004, about 8 percent. However, a sample of the first 100 generic names listed by Simpson compared with Anderson and Jones reveals changes involving 39 percent of them. Thus, changing concepts and content of mammalian genera not only occurs, but does so at a rate of two or three a year. Obviously, taxonomists note, absorb, and utilize these refinements and modifications without undue stress, confusion, or dissension. A desire to maintain the status quo in the face of new evidence and analysis is unscientific and unprofessional.

In the absence of reproductive data, most genera will continue to be distinguished on morphological evidence. It is noteworthy that, in estimating the "gap" between species or species-groups in formulating genera, excessive attention seems to have been paid to sexual dimorphism and conspicuous external features. If taxonomists have consciously or subconsciously guessed whether or not they thought the amount of morphological difference they observed was beyond the level of reproductive compatibility, they seem to have erred particularly in the highly dimorphic bovids, cervids, and cercopithecids. In practice, of course, most mammalogists would agree that many species in these families may generally be identified far more readily by examination of adult males than adult females, and by their external characters more readily than by skulls or teeth. Females of these groups, on the other hand, are often much more difficult to identify, mainly because the criteria for "generic" distinction are largely if not entirely based on dimorphic male attributes.

It is generally conceded that taxa of a given category in different phyla of animals are not equivalent, the most uniform perhaps being the species (Schaefer, 1976). Even within a group such as the class Mammalia, the higher categories in one order may not be the equivalent of those in others. In this context, it is particularly interesting to note that essentially all of the genera involved in hybridization are of animals that are largely diurnal. In these the species-isolating mechanisms seem to be based importantly on visual identification, and a high degree of social complexity and sexual dimorphism has developed. The ready discernment and conspicuousness of these identifying characteristics seems to have biased taxonomic judgment to grant these species higher taxonomic status than they may merit on actual evolutionary grounds or in relation to the taxonomic levels of other groups of mammals. Conversely, the genera of mammals with 40 or more species that I listed on p. 19, mainly are genera that are nocturnal and in which there is little sexual dimorphism. Vision probably plays a minor role in species-identification or social behavior in these, and in the absence of marked external differences, taxonomists have tended not to split them into genera as readily as they have divided other groups.

I have avoided consideration of how taxonomists of groups other than mammals deal with intergeneric hybrids or the level of the genus. However, it is noteworthy that many mammalogists regard the taxonomy of birds—a mainly diurnal and extensively dimorphic class—as being over-divided at higher categories. Naturally occurring intergeneric hybrids are far more common in birds than in mammals (Gray, 1958; Cockrum, 1952; and Short, 1969).

A lingering problem that remains from the use

of data on reproductive compatibility to delimit genera is the status of subgenera. By strict interpretation, subgenera as well as genera should not be capable of hybridization, if the species remains as the taxon distinguished by reproductive isolation. The utility of the subgenus is unquestioned, however, as a formal expression of morphologically similar and related species. There are other terms, of course, such as allospecies, superspecies, or species group which, in one form or another, express the idea of a closer proximation of the included taxa to one another than to other species or groups within the same genus. It seems appropriate now to apply the restriction of reproductive isolation to subgenera, as well, even though this will undoubtedly make more difficult the transition of the taxonomic changes proposed here. I have already stated that I believe that a genus, by definition, should include species that are incapable of breeding with those of any other genus. We already have the criterion that offspring, if any, of crosses between species should be sterile or have greatly reduced fertility. These definitions leave little space for an objective definition of other categories in the interstices between the level of the species and that of the genus.

In actual practice, the taxonomic changes suggested here that are determined by reproductive data are not novel. Most of them have been proposed by other taxonomists in the past, largely on morphological similarities. Resistance to their acceptance has been based less on the taxonomic or evolutionary consideration than on the desire to retain a familiar appellation, especially in nontaxonomic fields. The retention of *Thalarctos* for the polar bear, and of *Mandrillus* for the mandrills in much of the popular and applied literature are cases in point.

The definition of the genus has received far less attention than that of the species. Although chapters and even volumes are devoted to the concept of the species, the genus has usually received little more than a few lines or a paragraph or two. Winge (1941) is one of the few mammalogists who attempted to consider the genus as a uniform taxonomic level within the class, and interestingly, his genera often anticipate the data from intergeneric hybrids. He did not, however, define the genus.

From the evolutionary viewpoint, when species are grouped into a genus they are usually considered to have reached a new adaptive zone. From the presumed isolation provided by speciation, a species can then, without further genetic mixture with its near relatives, evolve to exploit a new environment or niche. When the morphological changes in adaptation to this new field reach a stage where the appearance or difference is greater than between most of the other species in the group, the species may be considered to be a genus.

In dealing with sympatric or contiguous species that do not interbreed in nature but do hybridize (even with fertile offspring) in artificial situations, such evidence is construed as further support for the specific validity of each of the species. Allopatric or allochronous species that can be hybridized with fertile offspring (under artificial conditions, of course) are generally considered to represent only subspecies because they are potentially capable of interbreeding. Most of the mammals that had been considered genera but were known to hybridize in nature have generally by now been relegated to congeneric status. Genera that are capable of hybridization and the production of a living offspring under artificial conditions form a case that is not unlike that of allopatric species or even sympatric species that do not interbreed in nature, but do in captivity. For intergeneric hybrids, fertility of the offspring need not be a criterion for evaluation of the status of the taxa. Sterility would indicate only that the parents of an intergeneric cross are good species; fertility would suggest that they are conspecific. I have somewhat arbitrarily selected the production of a living offspring as the criterion for acceptability in an intergeneric cross. It seems to me that if the chromosomes of two taxa are compatible enough to develop a fetus to term, then the parents would seem to be more closely related than generic separation would suggest. The viability of the offspring after birth has not been considered, partially because there is no way of determining how survival might be related to the animal's genetics. Survival of captive-born animals is often low, even when intertaxa crosses are not involved.

The relationships of reproductive capability to taxonomic levels, as I construe them, are:

Taxon	Can interbreed and produce fertile offspring	Can interbreed but produce sterile offspring	Cannot interbreed
Subspecies	Yes	No	No
Species, Sympatric	No	Some	Yes
Species, Allopatric	No	Some	Yes
Species, Sibling	No	?	Yes
Genera	No	No	Yes

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